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Department of Wildlife, Fish, and Environmental Studies

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Master´s thesis • 30 credits

Examensarbete/Master's thesis, 2018:7

Department of Wildlife, Fish, and Environmental Studies

Umeå 2018

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Credits:	30 credits
Level:	Second cycle, A2E
Course title:	Master degree thesis in Biology at the Department of Wildlife, Fish, and Environmental Studies
Course code:	EX0633

Place of publication:	Umeå
Year of publication:	2018
Cover picture:	J. Boer
Title of series:	Examensarbete/Master's thesis
Part number:	2018:7
Online publication:	https://stud.epsilon.slu.se

Keywords:	Pied flycatcher, Ficedula hypoleuca, temperature, breeding success, microclimate, nest box

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Abstract

Benefits in terms of breeding success might arise from selecting nest sites with warmer thermal conditions. These energetic gains can subsequently be invested in increased breeding success by both parents and their nestlings. This could be of increasing importance when breeding in colder climates, where lower temperatures can impose limits on breeding outcome. Forest restoration treatments (prescribed burning and gap cutting) previously carried out in our study area in northern Sweden have led to differences in temperature. Along this natural thermal gradient the relationship between temperature and breeding success of Pied Flycatchers (*Ficedula hypoleuca*) were studied. To test thermal effects of different life stages, temperature data was divided into the nesting (i), egg-laying (ii), incubation (iii) and nestling stage (iv). Results obtained in this study suggests that birds had mainly benefited from increased temperatures. Warmer temperatures led to increased fledging success and larger clutch sizes. In addition, higher nest box temperatures during incubation were related to heavier fledglings. This suggests that birds are also successfully able to allocate energy from one breeding stage to another. Thermal variations facilitated by restoration treatments might thus prove a valuable tool to aid avian breeding success.

Keywords: Pied flycatcher, *Ficedula hypoleuca*, temperature, breeding success, microclimate, nest box

Contents

Introduction

Whether the breeding effort of a bird will turn out to be successful is dependent upon several factors. An important determinant in this process is the thermal nest environment, and thus nest site selection can turn out to have a pronounced effect on avian breeding outcome. Changes in microclimate temperatures during separate life stages in particular have shown to influence egg viability (Beissinger et al. 2005, Cook et al. 2003), laying sequence (Yom-Tov and Wright 1993) and timing of egg-laying (Saino et al. 2004, Vedder 2012). The amount of energy that is invested by breeding birds in egg-laying (Nager and Noordwijk 1992) and incubation (Ardia et al. 2009) is also affected by temperature.

During breeding, temperature most notably is of importance when time devoted to brood care by parents comes at the expense of their own energetic needs. The incubation period is regarded as energetically costly (Ardia and Clotfelter 2007, Haftorn and Reinertsen 1985, Nilsson et al. 2008, Reid et al. 2000, Thomson et al. 1998, Williams 1996). However when temperatures fall below lower critical values of 15 °C have shown to lead to a substantial increase in energy expenditure in incubating Blue Tits (*Cyanistes caeruleus*) (Haftorn and Reinertsen 1985). In addition birds will also need to invest increasingly more in self-maintenance by leaving the nest to forage during lower temperatures. This can have consequences for breeding success, since females are expected to keep eggs at appropriate temperatures in order to maintain egg viability (Haftorn 1988). Warmer nest conditions typically relieve energetic constraints on females who in turn are able to modify their behavior accordingly. This is mainly expressed as an increase in effort invested in egg incubation and fewer interruptions in laying during warmer temperatures (Ardia et al. 2009, Ardia et al. 2010, Nord and Nilsson 2011, Olson et al. 2006).

Apart from the incubation period, the effect of nest temperature can also have consequences for reproduction during other life stages, such as the egg-laying period. Also known as the ‘energy limitation hypothesis’ (Perrins 1970), lower temperatures can alter both timing and egg formation by limiting the amount of

energy which a female can spend on both self-maintenance and egg production. Typically warmer nests during the egg-laying period can increase the amount which parents are able to invest in egg-laying, leading to earlier hatching and fewer interruptions in egg-laying (Bleu et al. 2017, Vedder 2012, Yom-Tov and Wright 1993). However, birds might also respond to increasing temperatures by attempting to advance hatching in order to match with the peak of food availability (Visser et al. 1998). According to the latter hypothesis, higher temperatures should therefore lead to smaller clutch sizes by minimizing the risk of mismatch. The lack of increase in clutch size during the season (Bleu et al. 2017, Nager and Noordwijk 1992, Vedder 2012, Yom-Tov and Wright 1993) and lack of carryover effects on older nestlings shown in Bleu et al (2017) and Vedder (2012) suggests that birds perceive warmer conditions during egg-laying as cue for seasonal advancement, rather than the removal of an energetic constraint. Whether earlier hatching can be regarded as an attempt to coincide hatching with food availability or the result of lowered energetic constraints, or perhaps a combination of both, is still debatable. Nonetheless timing can have important consequences for breeding outcome. Declines in overall breeding success during the season been well documented and is mostly attributed to lowered prey abundance (Haartman 1982, Harvey et al. 1985, Lundberg et al. 1981, Siikamäki 1998).

Trade-offs between self-maintenance and brood care can also have consequences on nestlings during later life stages (Ardia et al. 2010, Bleu et al. 2017, Heany and Monaghan 1996, Hepp and Kennamer 2012, Perez et al. 2008). Even though young Tree Swallow (*Tachycineta bicolor*) nestlings from experimentally warmed nests were found to have better body condition, the best indicator for increased body condition of older Tree Swallow nestlings was whether or not the female had been heated during incubation (Perez et al. 2008). Females originating from these nests were found to provision their young at a higher rate. Similarly, studies have found that nestlings provisioned by females that had incubated in cooled nests had lower body mass later on in the nesting stage (Ardia et al. 2010, Nilsson et al. 2008). The well documented negative effect of lower incubation temperatures on early hatchling body condition (Ardia et al. 2010, Hepp et al. 2006, Martin et al. 2007, Nilsson et al. 2008), which is most likely caused by a reduction in embryonic development (Olson et al. 2006), can thus potentially be compensated for throughout stages later in life.

While these carry-over effects between separate life stages have been reasonably well documented, the direct relationship between overall breeding success and microclimate temperature conditions however, still remains somewhat ambiguous. In several field studies, a preference for south facing nest boxes have been shown by several bird species (Rendell and Robertson 1994). Most likely, to benefit from in-

creased sun exposure especially at higher latitudes (Burton 2007). As a result, research linking overall breeding success and temperature has therefore mainly focused on thermal microclimate differences in correlation to nest box orientation (Ardia et al. 2006, Butler et al. 2009, Charter et al. 2010, Rauter and Reyer 2000, Rendell and Robertson 1994). Microclimate conditions between sites might however vary independently from orientation due variable levels of sun exposure and canopy cover. A small number of correlative studies however have examined breeding success in direct relation to nest thermal environments with various results. In British Colombia, only clutch size, but not hatching or fledging success in Northern Flickers (*Colaptes auratus*) was found to be positively correlated with temperatures in natural cavities (Wiebe 2001). Natural cavities with fledged Mountain Chickadees (*Poecile gambeli*) experienced higher temperatures compared to those which were unsuccessful (Wachob 1996). Fledging success of Tree Swallows declined when exceeding high (35 °C) temperatures during daytime, but was positively correlated with night-time temperatures (Ardia 2013). Overall, this corresponds with the notion that lower temperatures imposes severe energetic costs, while nestlings subjected to temperatures exceeding the thermo-neutral zone may be at risk for hyperthermia (Mertens 1977, Salaberria et al. 2014).

In colder climates temperature will presumably play an increasingly important role in breeding success, particularly when considering the higher energetic costs of reproduction associated with higher latitudes (Järvinen 1983). In Fennoscandia colder breeding conditions and sudden temperature fluctuations are not uncommon, especially during the early part of the season. Selecting a specific microhabitat might prove to be advantageous, even more so for smaller passerine species. Forestry practices in Sweden have resulted in a decline of naturally occurring disturbances as well as less variation in age and composition of vegetation. Accordingly, these areas also accommodate less variation in microhabitat. As a restoration effort, recent treatments such as gap cutting and prescribed burning have been carried out to increase biodiversity. Versluijs et al. (2017) demonstrated differences in both (living) tree density and basal area between study sites four year after treatment. Conducted in the same study area, this has created a unique opportunity for our study to examine the possible effects that might arise from these natural thermal variations. The Pied Flycatcher (*Ficedula hypoleuca*) was selected as a species for this study due to its abundance and extensively studied natural history. It is primarily a secondary cavity breeder, but willingly accepts nest boxes (Balen et al. 2002).

This study aims to assess whether differences in temperature between nest boxes will affect reproduction of Pied Flycatchers in Northern Sweden. By equipping nest boxes with temperature loggers, we attempted to measure the consequences of these thermal variations between nest boxes on parameters of reproductive success (clutch size, number of hatchlings, hatching success, nestling weight and tarsus length,

number of fledglings, fledging success). In addition, to control for parental quality, morphological traits (weight and tarsus length) of breeding adults were used as covariates. To determine the effects of temperature during different stages of reproduction, temperature data was split into four separate stages: i.) nest, ii.) egg-laying, iii.) incubation and iv.) nestling stage.

Colder environments can impose limitations on breeding success. Nests receiving more sun exposure due to restoration treatments, are expected to have higher breeding success. Effects of nest temperature are not straightforward to predict, since carry-over effects can take place and can affect both parent and offspring. Mainly the prediction is that reduced energetic costs for maintenance (Ardia et al. 2009, Ardia et al. 2010, Nord and Nilsson 2011, Olson et al. 2006) in warmer nests will allow parents to invest more in brood care. This increase in parental effort will most likely be reflected by increased in either nestling body condition or higher fledging success.

Material & methods

Study area design

Data were collected from 30 study sites located in Västerbotten and partly in Västernorrland in northern Sweden (63°23´N to 65°02´N and 16°80´E to 21°20´E, Figure 1). Study site sizes varied between 3 and 25 ha. The most dominant tree species found were Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Deciduous trees made up at least 10% of trees within our study sites and the most prevalent species included: silver birch (*Betula pendula*), downy birch (*Betula pubescens*), European aspen (*Populus tremula*), grey alder (*Alnus incana*), willow species (*Salix sp*.) and rowan (*Sorbus aucuparia*). All study sites (with the exception of one state protected burned area) were voluntarily set aside by a forest company (Holmen AB) as part of their FSC-certification. These sites had previously undergone restoration treatments in 2011: artificial gap cutting and prescribed burning. In addition, unmanaged areas served as control sites. Ten sites for each treatment were included in this study. In sites which received gap treatment, circular gaps of approximately 20m in diameter were cut around a single tree. This resulted in 6 gaps per ha, covering approximately 19% of every site. In 50% of these gap treatment sites trees were subsequently left as dead wood while the remaining 50% was removed to account for costs involved. Prior to burning treatment 5-30% of the trees (mainly spruce) were removed to serve as timber as well as to ensure drier forest floor conditions. Approximately 2-5 m3/ha of cut trees were left to function as fuel.

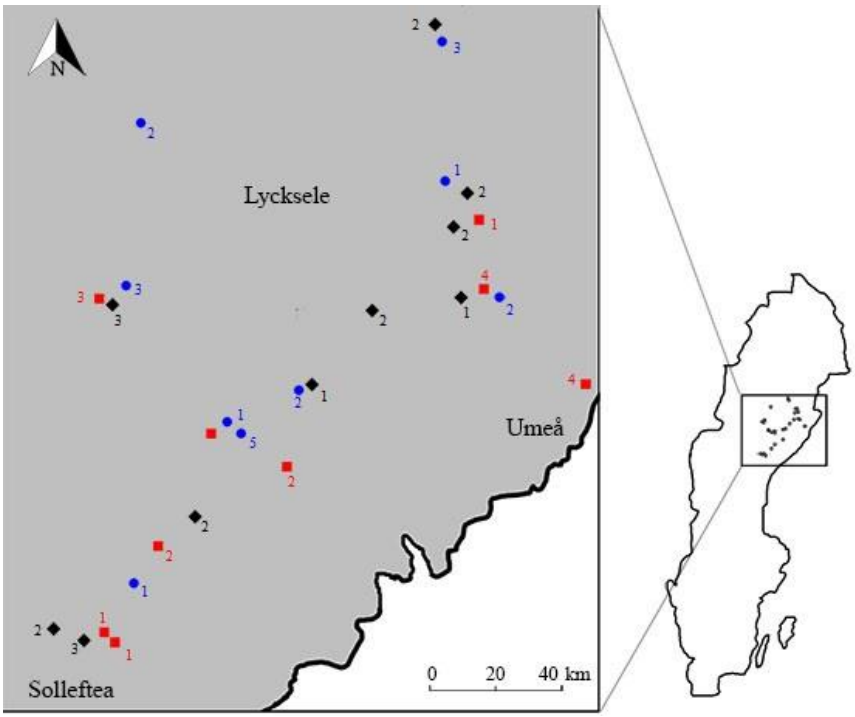

Figure 1. Study area in northern Sweden. Burned study sites are marked by red squares, gap sites by blue diamonds and the control sites by black circles. Numbers within the symbols represent the number of nest boxes equipped with temperature loggers within a particular site. Note that two sites were ultimately excluded due to insufficient breeding pairs.

Nest boxes

Within the study sites, a total of 184 wooden nest boxes were placed during the autumn of 2015. Nest boxes were placed at a height of 1.3m, separated by at least 80 m. and placed in low densities, approximately 1.5 ha per nest box. Taking into account that distance to forest edge is also related to breeding success in Pied Flycatchers (Huhta et al. 1999), nest boxes were placed from a sufficient distance away from the outer edges (at least 50m.) of the study sites. Nest boxes were placed facing southwards. Although nest boxes might not necessarily reflect natural conditions (Maziarz et al. 2017) they do provide an excellent opportunity to control for location as well as entrance orientation.

Data collection

Breeding data

Starting from mid-May 2017, all nest boxes were visited at least once every week to determine laying date, clutch size and start of incubation. Date of laying was determined by counting back from the clutch size which was encountered, under the assumption that one egg per day was laid. Assuming that incubation would start at the very same day as clutch completion, the date at which the last egg was laid was subsequently marked as the start of incubation. The nests were visited shortly after the estimated hatching date (marked day 0) to observe the number of hatchlings, and with the aid of a provided field chart (Vogeltrekstation 2013) nestling age was determined as well. Nestling weight and tarsus were recorded before fledging, between day 10 and 14. A digital scale was used to measure weight to the nearest 0.1 g and tarsus was measured (from the "notch" of the tarsal joint, excl. the tibiotarsus) with a digital calliper to the nearest 0.01mm. For each individual, the average of three tarsus measurements were taken and subsequently averaged to minimize the risk of measurement errors. We attempted to catch both parents with either mist nets or directly in the nest box to likewise measure both their weight and tarsus. Sex determination of adult birds was done by confirming either the presence or absence of a brood patch as well as plumage colour, forehead patch and the wing and tail pattern (Svensson 1992). Since differences in breeding success can also be attributed to age (Huhta and Jokimäki 1998) adult birds were divided into two age classes: first year breeder or older birds (Lundberg and Alatalo 1992). Adult birds were also ringed with an aluminium ring. By providing a means of identification we aimed to minimize the chance of including nests with lower nestling quality as a result of male polygyny (Alatalo et al. 1981). Ringing was only carried out if nestlings were at least 4 days old in order to limit the risk of parents deserting the nestlings. Once the nest was considered completed (i.e. after the age of 15 days) a final check was performed to establish the number of fledged chicks and possible mortality.

Figure 2. Nest box with two attached temperature loggers, one directly under, and one placed inside the nest box.

Nest box temperature recordings

60 nest boxes were equipped with temperature loggers (Thermochron iButton® DS1921G, Maxim integrated, USA, accuracy ± 1°C, 17 × 6 mm, 3.3 g) which measured at 0.5 °C increments. Temperature loggers were distributed as equally (20 per treatment) and randomly as possible amongst treatments and study sites. After species identification, confirmed by the presence of a singing male Pied Flycatcher and nest characteristics, nest boxes were equipped with two temperature loggers (Figure 2). With the exception of four nests which already contained eggs, all loggers were placed during the nesting period. The first logger was placed at the back and above the nest to record internal temperature, hereby referred to as 'nest box temperatures'. Another logger was then placed 10-15 cm under the nest box to record external temperature, which will be referred to as 'ambient temperatures'. A small (⌀ +/- 6 cm), clear plastic cup also provided additional cover from rainfall for the external temperature logger. Data loggers were set to record temperature (°C) at a one hour time interval. The first and final day of recording were not included in the analysis.

Statistical analysis

One nest out of 60 was excluded entirely prior to temperature analysis, since this nest had fledged before breeding data could be collected. None of the nestlings were lost as a result of predation. Weight and tarsus data of 295 nestlings from 55 nest boxes were included, as well as 22 adult males and 39 females. Out of these measurements, four female tarsus measurements, which were possibly inaccurate due to faulty equipment early on, were eventually not included.

Temperature data

Since the egg-laying, incubation and nestling period were determined for each nest, we were able to divide nest box temperature data into four separate periods: i) nesting, ii) egg-laying, iii) incubation and iv) nestling stage. For each nest box, the average temperature was calculated for each of these stages. In addition to the average temperature, the average of the maximum (corresponding with day-time temperatures) and minimum temperature (corresponding with night-time temperatures) of each day were also calculated for each stage. This was done for both internal and ambient temperature. For each nest box the period which was included to calculate the average, minimum and maximum temperatures for each different stage was determined as follows:

i. To calculate the temperature during the nest stage (i), the average, minimum and maximum temperature of two days prior to the day at which the first egg

was laid were taken. The exact date of the first egg was determined by counting back from the encountered clutch size minus one.

ii. The egg-laying stage (ii) consisted of the average, minimum and maximum temperature starting from the day at which the first egg was laid until the start of incubation. If exact onset of incubation could not be determined the number of days were defined as the final clutch size. One day was subsequently extracted under the assumption that incubation would start on the same day as clutch completion.
iii. The incubation stage (iii) consisted of the average, minimum and maximum temperature from the start of incubation until the first egg had hatched. 14 days were maintained when exact onset could not be determined.
iv. The nestling stage (iv) consisted of the average, minimum and maximum temperature from the day the first egg had hatched until fledging. A total of 16 days were maintained when exact date of fledging (or hatching) could not be determined.

For the nest stage (i) 16 out of 59 nests were eventually excluded since at the start of recording the nests either already contained eggs or only recorded only one day prior to egg-laying. Due to abandonment, 56 nests contained data for the egg-laying stage and 54 nests contained data for both incubation (iii) and nestling (iv) stage. Ambient and internal temperature variables for each stage were tested for collinearity using Pearson's r, assuming correlation is present when $r_s > 0.7$ (Dormann et al. 2013). All ambient and internal nest box temperatures showed correlation ($r > 0.7$) with the exception of average ($r = 0.66$) and minimum ($r = 0.69$) temperature during the nestling-stage (iv). To test for differences in average, minimum and maximum nest box temperatures between restoration treatments an ANOVA and a Tukey pairwise post hoc were used.

Model structure

To determine the effect of temperature on breeding success, nestling weight and tarsus, clutch size, number of hatched chicks, number of fledged chicks, hatching success and fledging success were used as response variables. Hatching success was defined as the number of hatchlings divided by clutch size. Fledging success was calculated by dividing the number of fledglings by the number of hatchlings. For every model a fixed number of explanatory covariates were added. A more detailed overview of variables which were used is shown in Appendix I. Firstly, as a proxy for the quality of the parent, we used female and male tarsus, age and weight. Since including adults (due to the low amount of birds caught) would greatly diminish our available dataset, variables for parental quality (weight, age and tarsus) were tested

separately. Since factors for parental quality did not have any significant effect on any of the response variables these were was excluded from any further analysis. Secondly, temperature was added as an explanatory variable. Since several temperature variables were correlated each of the temperature variables were tested separately against every response variable. Temperature variables were added when deemed biologically relevant e.g. temperature during nestling stage (iv) was not tested for the response variable clutch size. The total basal area surrounding each nest box was added as a proxy for habitat structure. Total basal area was previously collected in 2015 (data unpublished), and included basal areas of live trees (⌀>5cm) in a radius of 10m for coniferous and 35m for deciduous trees around each nest box. In addition we added nestling age and brood size at time of weighing as a covariate for nestling tarsus and weight. The study site was included as a random effect since some nest boxes occurred within the same study site. In addition spatial auto-correlation was added since study sites were distributed over a large area. This was tested with either a linear mixed model (LMM, lme function from the "lmer" package) or a generalized linear mixed model (GLMM, glmer function from the "lme4" package). Study site and spatial-auto correlation did not improve the fit of the models and were therefore excluded from the final models. Non-significant variables were subsequently removed using backward elimination.

To test the effect of temperature on nestling weight, a LMM was used. Nest box was added as a random factor to account for the fact that several nestlings originated from the same nest. Nestling tarsus was similarly modelled with a linear mixed model, adding nest box as a random factor. Assumptions of normality and homogeneity of variances were fulfilled. Clutch size, number of eggs hatched (≥1) and number of fledged chicks (≥1) per nest box were used as response variables and modelled with a generalized linear model using a quasi-poisson distribution. A GLM with quasi-binomial distribution was used for hatching success as well as fledging success.

In addition to testing for temperature effects on breeding variables, differences in fledging success according to average weight per nest box were also tested with a similar model using the entire dataset (n=112). The entire data-set, including all nest boxes with breeding Pied Flycatchers (n=158), was used to test for possible differences in clutch size depending on laying date using a generalized linear model (GLM) with quasi-poisson distribution. A similar model was used to test for the effect of laying date of the number of fledglings. The effect of laying date on both hatching and fledging success were similarly tested by using a GLM with a quasi-binomial distribution to correct for overdispersion. For the laying date, modified dates were used which started at the 1st of May (e.g. 1st of May =1, 1st of June = 32 etc.). Differences were considered significant at $p < 0.050$. All statistical analysis were performed using R version 3.4.1 (R Core Team 2017).

Results

Treatment and temperature

Average, maximum and minimum nest box temperatures were significantly different between treatments (ANOVA $F_{2, 51}$=15.48, p <0.001, $F_{2, 51}$=24.50, p <0.001 and $F_{2, 51}$=3.20, p = 0.049 respectively). Study sites which had undergone burn treatment had nest boxes with significantly higher average, maximum and minimum temperatures compared to control and gap treated areas (Figure 3). Burned sites also differed significantly in minimum temperature from gap treated areas. Nest boxes did not show a difference in buffering capacity (i.e. the difference between internal and ambient temperature recordings their maximum and minimum temperature difference) between treatments ($F_{2, 38}$ = 2.408, p = 0.104).

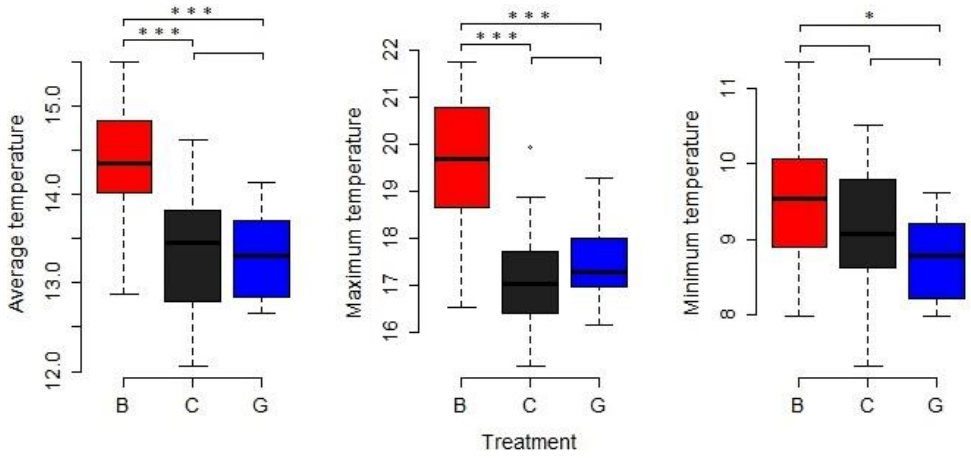

Figure 3. Differences in nest box average, maximum and minimum temperature (°C) between treatments from nest (i) to nestling-stage (iv). Burned (B) areas are shown in red, control areas (C) in black and gap (G) areas in blue. Temperatures shown are those recorded inside the nest boxes. Asterisk (*) indicates significant p-values (*p <0.050). ** p <0.010, *** p <0.001).

Effect of laying date on breeding success

No difference was found between earlier and later breeders in this study. Laying date had no significant effect on clutch size (GLM, $F_{1, 154}$= 2.3314, p = 0.129) or hatching success (GLM, $F_{1, 151}$= 0.050, p = 0 .944). Breeding date (date of first egg) did not have any significant effect on nestling weight (LMM, with nest box as random effect $F_{1, 242}$= 0.19, p = 0.551). Using data from all breeding Pied Flycatchers, fledgling success (GLM, $F_{1, 145}$= 2.89, p = 0.108) nor number of fledglings (GLM, $F_{1,141}$= 0.38, p = 0.540) were found to be affected by start of egg-laying, i.e. earlier breeders did not differ significantly from later breeders in terms of fledging success or fledglings.

Effect of temperature on breeding success

Clutch size, number of hatched eggs and hatching success

Clutch size was positively affected by average nest box temperature during the egg-laying period (Table 1). No other predictors initially included in the model predicted clutch size. Temperature did not have any effect on either the number of hatched eggs or hatching success (all temperature variables p >0.050).

Table 1. *Model outcome from the generalized linear model showing clutch size as predicted by nest box maximum temperature during egg-laying (ii). A quasi-poisson distribution was used. Asterisk (*) indicates significant p-values (<0.05).*

	Dependent variable in model			
Predictors	Clutch size			
	Estimate	SE	*t*-value	P
Intercept	1.56	0.13	12.38	<0.001*
Max. temp. during egg-laying (ii)	0.02	0.01	2.44	0.018*

Nestling weight and tarsus length

Weight of nestlings was shown to be significantly affected by nest box maximum temperatures during incubation (LMM, $F_{1, 241}$=2.39, p = 0.044, Table 2, Figure 4). Average nest box temperature did show a similar trend with nestling weight, albeit non-significant (LMM, $F_{1, 241}$= 1.56, p = 0.068). Minimum incubation temperatures in the nest box did not have an effect on the weight of nestlings (LMM, $F_{1, 241}$= 0.02, p = 0.791). None of the temperature variables were shown to have any effect on the average nestling tarsus length per nest (all temperature variables p >0.050).

Table 2. *Linear mixed model of nestling weight with maximum temperature during the incubation-stage (iii), nestling age and brood size at time of weighing as predictors. Nest box was used as a random factor. Asterisk (*) indicates significant p-values (<0.050).*

	Dependent variable in model			
Predictors	Nestling weight			
	Estimate	SE	*t*-value	P
Intercept	11.97	1.26	9.48	<0.001*
Max. temp during nest - stage (i)	0.08	0.04	2.01	0.044*
Nestling age	0.13	0.10	1.29	0.089
Brood size	-0.21	0.06	-3.58	<0.001*

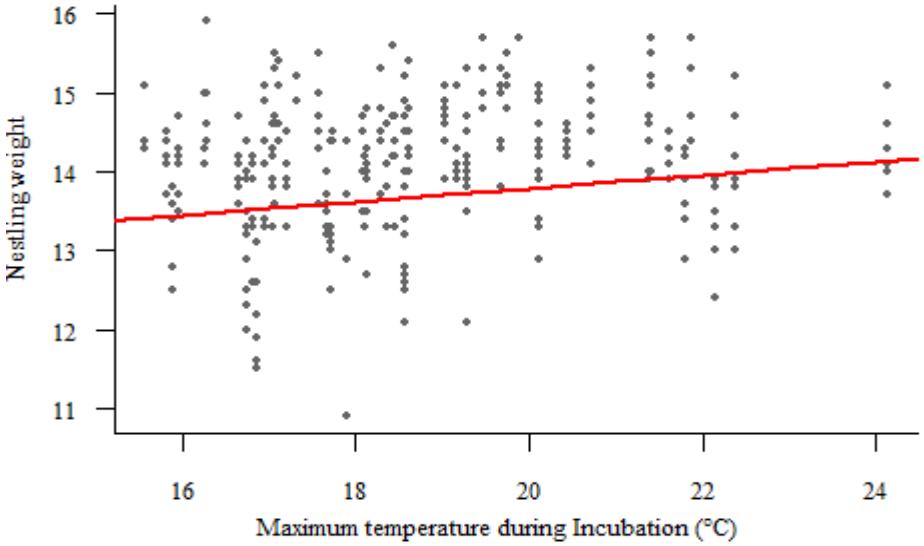

Figure 4. Nestling weight (in grams) according to maximum nest box temperatures during incubation (iii). The slope is an estimate of the linear mixed model shown in Table 2. Nest box was used as a random factor.

Number of fledglings and fledgling success

Fledging success was significantly lower in nests which had a lower average nestling weight, even when accounting for differences in brood size (GLM, $F_{1, 111}$= 3.64, p = 0.005, see also Appendix II). Nests also produced fewer nestlings when the minimum internal nest temperature during nestling-stage (iv) was lower (Table 3). However, effects of temperature on the number of fledglings might occur before the nestling-stage. Fledging success (being strictly the percentage of nestlings surviving from hatchlings to fledglings) gives us a stronger indicator of possible effects of

nest box temperatures happening primarily during the nestling-stage. When modelling fledging success, nests had significantly higher fledgling success at higher average nest box temperatures during nestling-stage (Figure 5, Table 3).

Table 3. *Generalized linear model of the number of nestlings fledged per nest and fledging success with total basal area and minimum nest box temperature during nestling-stage (iv) as predictors. A quasi-poisson and quasi-binomial distribution were used respectively. Asterisk (*) indicates significant p-values (<.050).*

	Dependent variable in model							
Predictors	Nestlings fledged				Fledging success			
	Estimate	SE	*t*-value	P	Estimate	SE	*t*-value	P
Intercept	1.10	0.32	3.40	0.001*	-12.28	7.70	-1.60	0.117
Min. temp during nestling - stage (iv)	0.06	0.03	2.16	0.036*				
Ave. temp during nestling – stage (iv)					1.02	0.53	1.91	0.040*

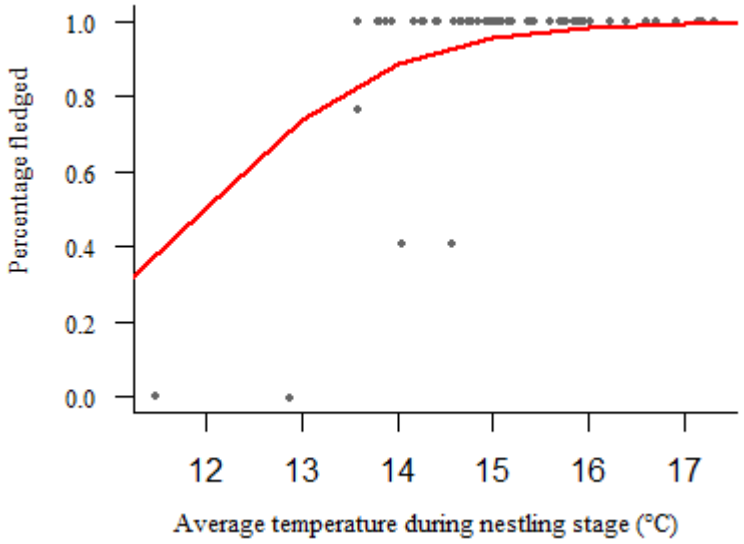

Figure 5. Fledging success a function of average temperature during the nestling stage (iv). The slope is an estimate of the GLM in Table 3.

Discussion

In this study we investigated thermal differences inside nest boxes and the subsequent effect on reproductive success of Pied Flycatchers breeding in a colder environment. Restoration treatments (burning, gap and control) which had been carried out in 2011 demonstrated significant differences in temperature in our study sites (Figure 3) and created a unique opportunity to study the subsequent effects on breeding outcome. In general, Pied Flycatchers gained from warmer temperatures by showing an increase in clutch size, fledging success and nestling mass when experiencing warmer nest box conditions.

A positive effect of warmer nest box temperatures during egg-laying on clutch size was observed. While birds sometimes use warmer temperatures as a cue to advance breeding with food supply (Bleu et al. 2017, Visser et al. 1998), this is not reflected in the results obtained during this study. Had birds attempted to match hatching with food supply in accordance with warmer temperatures, a reduced clutch size to forward hatching would have been expected. We would have expected to see smaller clutch sizes at warmer temperatures since birds would attempt to coordinate (and speed up) hatching with the peak of food abundance. This is also reflected by the absence of a decline in breeding success overall in this study, as also no effect of laying date was found on hatching and fledging success, number of fledglings or nestling weight. A decline in breeding success as the season progresses is well-documented in Pied Flycatchers (Haartman 1982, Lundberg et al. 1981), so an absence of this phenomenon might seem unusual. A decline in breeding success seems to largely be the result of reduced food supply later on in the season (Lundberg and Alatalo 1992, Siikamäki 1998). However, it is mostly associated with oak (*Quercus spp.*) habitats and warmer years since in those habitats the seasonal decline in caterpillars is much steeper (Burger et al. 2012, Veen et al. 2010). Our study area mostly consisted of coniferous trees which most likely explains the absence of any sort of reduction in breeding success as the season progresses. However it can also be attributed to seasonal variation (Järvinen 1993, Siikamäki 1998). Our results seem to be more in favor of higher temperatures reducing energetic costs

which allows females to invest more in breeding, such as laying more eggs (Perrins 1970, Reid at al. 2000, Yom-Tov and Hilborn 1981). The relationship between clutch size and temperature may be an artefact of the probability that higher temperatures are positively correlated with food abundance, thus increasing parental condition during egg-laying (Martin 1987). However, studies which manipulated nest temperatures have shown that females benefit from higher temperatures resulting in lowered energetic costs and subsequently investing in clutch size (Reid et al. 2000, Yom-Tov and Hilborn 1981), independent from food supply. Moreover, a study by Eeva et al (2002) which compared two Pied Flycatcher populations found that those breeding in colder climates responded adaptively to lower temperatures by reducing their clutch size. Temperature might directly affect energy expenditure of the female, or indirectly by correlating with food abundance. Regardless, our data indicates a positive correlation of temperature with clutch size.

The results also suggest a carry-over effect between life-stages, were incubation temperatures in the nest box affect nestling mass. Similar to clutch size, it can also not be excluded that the higher nestling weight is also indirectly due to the fact that temperatures correlate with insect abundance (Drent 1973) resulting in increased female body reserves (Martin 1987). Aerial insects, the main diet of the Pied Flycatcher (Lundberg and Alatalo 1992), tend to hide among vegetation in temperature conditions below 10°C (Taylor 1963, Veistola et al. 1997). An increasing body of evidence however, reveals that incubation is energetically costly, and temperature directly affects female energy expenditure (Ardia and Clotfelter 2007, Haftorn and Reinertsen 1985, Nilsson et al. 2008, Reid et al. 2000, Thomson et al. 1998, Williams 1996). Studies manipulating nest temperatures have shown that, once relieved of energetic restrictions, birds in warmer nests increase incubation effort (Aminasab et al. 2016, Bryan and Bryant 1999, Conway and Martin 2000) as well as an increase in female body mass (Ardia et al. 2009, Perez et al. 2008). As a result, this can subsequently carry over to fledglings, leading to increased nestling body conditions (Ardia and Clotfelter 2007, Perez et al. 2008, Vaugoyeau et al. 2017) and higher fledging success (Ardia 2013). While studies have attributed this to increased provisioning rates resulting from reduced maintenance costs for the incubating female (Perez et al. 2008), warmer incubation temperatures have also shown to directly affect embryonic conditions and subsequently nestling mass, but this is usually documented in younger nestlings (Ardia et al. 2010, Hepp et al. 2006, Martin et al. 2007, Nilsson et al. 2008, Olson et al. 2006). A study on Tree Swallows by Perez et al. 2008 similarly found that chicks from experimentally warmed nests were heavier close to hatching. Regardless of the treatment which the nestlings had received however, older chicks close to fledging were heavier when fed by females from experimentally warmed nests due to increased provisioning rates. Experi-

mental studies that warmed nests whilst the female incubated have similarly demonstrated increased nestling body conditions close to fledging (Perez et al. 2008, Reid et al. 2000) or higher fledging success (Ardia 2013). While both artificial incubation (directly affecting embryonic conditions) and warmed nests (which additionally also affects female behavior) seemingly have consequences for nestling body condition, the increase in weight in older nestlings found in this study are thus seemingly more in favour of the theory that energetic relieve experienced by the female is subsequently invested in brood care, rather than a result of increased embryonic conditions. This is further reinforced by several studies with artificially incubated eggs which did not demonstrate any difference in weight of older nestlings (Berntsen and Bech 2016, Hepp and Kennamer 2012, Nord and Nilsson 2011, Nord and Nilsson 2016).

Admittedly not all studies manipulating incubation temperatures for both female and eggs have found differences in nestling morphology close to fledging (Vaugoyeau et al. 2017). Drawing general conclusions regarding temperature effects during incubation on nestlings remains difficult due to the variety of methods used in experimental studies. Artificial incubation permits testing along a temperature gradient whilst neglecting to take into account the thermal effect on the incubating female. Experimentally warmed nests (mostly with hand warmers) provide a more comprehensive view but limit studies to only one experimental group and use a variety of methods which for instance differ in temperature range and length and timing of treatments (Ardia et al. 2009, Ardia et al. 2010, Perez et al. 2008, Reid et al. 2000, Vaugoyeau et al. 2017). Restoration treatments which were carried out prior to this study provided an opportunity to test along a thermal gradient which reflects more natural conditions. The results also demonstrate effects of incubation temperatures on later nestling weight. This might also have implications for future survival since increased weight at fledging is generally associated with higher chances of survival into adulthood (Both et al. 1999, Lundberg and Alatalo 1992, Rodriguez et al. 2016, Tinbergen and Boerlijst 1990).

Additionally, while warm temperatures were correlated with increased nestling weight, no such relationship was found between minimum temperatures and nestling weight. This contradicts several studies in which colder temperatures impose costs and show a negative relationship between nestling mass and incubation temperature (Ardia and Clotfelter 2007, Ardia et al. 2010). Pied flycatchers breeding in northern areas however, were found to be substantially better adapted to colder periods compared to their southern counterparts (Eeva et al. 2002). Possibly, the same holds true for the northern breeding Pied Flycatchers in this study and colder temperatures might impose little to no cost. It might be interesting for future research to see whether experimental cooling of nests might affect northern breeding species differently than those breeding in more southern areas.

Similar to this study, higher temperatures during the nestling-stage (iv) have shown to positively affect fledging success (Ardia 2013, Geiser et al. 2008). Increased thermal conditions during the nestling-stage have also shown to influence nestling growth (Järvinen and Ylimaunu 1986, McCarty and Winkler 1999, Pérez et al. 2016). Nest box temperatures can affect fledging success in a number of ways, mainly by 1.) affecting food supply and directly decreasing energetic demands of 2.) the female and that 3.) of the nestlings. Another factor that could influence fledging success is predation. However, loss due to predation was very low in this study (pers.ob). Pied Flycatchers are dependent on the mobility of their insect prey and have a lowered feeding frequency (1) during colder conditions which could directly affect fledging success (Geiser et al. 2008, Veistola et al. 1997). However, we found no correlation between nestling weight and nest box temperatures during the nestling stage that might support this. Nest box temperatures could also directly affect female energy reserves (2) but this is rather less likely since females spend considerably less time brooding after the nestlings are 3-5 days old (Lundberg and Alatalo 1992). Thus, this would only be relevant early on in the nestling period. The thermoregulatory abilities of nestlings, especially when younger, are limited (Mertens 1977, Perrins 1970). During colder temperatures, the energetic demand of maintaining body temperature increases frequently at the cost of growth (3) (Krijgsveld et al. 2003). Although studies manipulating temperature during the nestling period are quite scarce, warmer nests have shown to lead to enhanced survival (Dawson et al. 2005) and increased development (Rodríguez and Barba 2016) in nestlings. Temperature can thus have an effect on nestlings independent of food supply. Increased weight has been commonly linked to higher survival of nestlings (Both et al. 1999, Lundberg and Alatalo 1992, Tinbergen and Boerlijst 1990). Though no link between weight and thermal nest box conditions during the nestling phase were found, we did find a connection between weight and fledging success. Nests with lower fledging success were of lower average weight. Possibly a difference in food supply might have concealed any effect of temperature during the nestling stage on nestling weight. Another possibility could be that the thermal benefits were allocated to other traits affecting survival such as plumage development (Verhulst 1994). Nonetheless, the results of this study regarding fledging success must be met with some caution. Low nestling mortality during our study (only six nests displayed nestling mortality, of which only five contained temperature data during nestling-stage) made it somewhat difficult to present any strong differences between successful and less successful nests.

Although the data obtained during the course of this study is representative for Pied Flycatchers found at similar latitudes, fledging success can be highly variable between years (Lundberg and Alatalo 1992) especially in colder climates (Järvinen

1993, Järvinen 1979). This study should be regarded as preliminary and repeating this experiment would be necessary to account for variability between years. Also an additional measurement of food availability would provide a more thorough understanding of thermal effects separate from prey abundance. Due to logistical reasons, nestling weight was only measured closely before fledging. It would also be interesting for future research to investigate growth patterns of nestlings. This might provide additional insight in whether the increase in nestling body weight is perhaps (partly) due to an increase in provisioning or the result of the thermal environment affecting nestling development. Lastly, the results of this study might also not be readily applicable to birds breeding in natural cavities. While nest boxes provide excellent opportunities to control for height, orientation and breeding densities natural cavities do offer more efficient insulation (Maziarz et al. 2017). It might therefore be interesting to compare these results with similar observations in natural nests.

In this study we found patterns between breeding success and nest box temperatures of Pied Flycatchers breeding in a colder environment. In accordance with our initial hypothesis, birds seemed to have primarily benefited from warmer nest box conditions, showing an increase in clutch size, fledging success and nestling mass. Birds are also seemingly able to successfully allocate energy gained from one breeding stage and invest in another. The results of this study demonstrates a carry-over effect, with increased thermal nest box conditions during incubation carrying over to nestling body mass. Ultimately, the results of this study offers some insight into the effects of natural temperature gradients on the success of a nest box breeding bird. Especially in colder climates, it might prove advantageous to select warmer nesting sites. In our study, nest boxes from sites which had undergone prescribed burning led to higher temperatures compared to control sites. Restoration efforts thus might prove to be a valuable tool to improve avian breeding success.

Acknowledgements

I would like to thank Martijn Versluijs for the guidance and advice provided during this project and also for long driving hours that were committed to this study. I also want to express my gratitude to Jean-Michel Roberge for both the opportunity to work on this project and his supervision. My appreciation also goes out to Elias Forsberg for his help in collecting the breeding data.

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Appendix I

Table 4. *Table showing both the response and explanatory variables which were initially added to the model. Explanatory variables in italic were tested separately on each response variable (see methods section).*Temperature is split into different stages (see method section), **Brood size and nestling age at time of measurement, ***Parental quality variables are parental age, weight and tarsus.*

	Response variable						
Explanatory variable	Nestling weight	Nestling tarsus	Clutch size	Number of hatch-lings	Number of fledg-lings	Hatching success	Fledging success
Temperature*	x	x	x	x	x	x	x
Basal area	x	x	x	x	x	x	x
Brood size**	x	x					
Nestling age**	x	x					
*Parental quality****	*x*	*x*	*x*	*x*	*x*	*x*	*x*
Study site	*x*	*x*	*x*	*x*	*x*	*x*	*x*
Spatial auto correlation	*x*	*x*	*x*	*x*	*x*	*x*	*x*

Appendix II

Table 5. *Model outcome from the generalized linear model showing fledging success per nest. Predictors shown are the average nestling weight and brood size per nest box. A quasi-binomial distribution was used. Asterisk (*) indicates significant p-values (<0.050).*

	Dependent variable in model			
Predictors	Fledging success			
	Estimate	SE	*t*-value	P
Intercept	-11.56	3.15	-3.67	<0.001*
Average weight of nest	0.61	0.21	2.86	0.005*
Brood size	1.11	0.13	8.56	<0.001*

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